

Inter-population variation among *Ceratitis capitata* flies in host acceptance pattern

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Abstract

Significant inter-population differences in propensity to attempt boring into (accept) various types of fruit for oviposition were found among *Ceratitis capitata* females from two wild sources and one laboratory source. Evidence suggests that (a) fruit size had a strong influence whereas fruit taxonomic status had little influence on the acceptance pattern of each population, and (b) at least a portion of the inter-population variation had a genetic basis.

Introduction

The host location process of herbivorous insects may be described as a chain of events (Thorsteinson, 1960) involving several successive phases (Kogan, 1977): host habitat finding, host finding, host recognition, host acceptance, and host suitability. During recent decades, a rather large volume of research has illuminated numerous sorts of positive and negative chemical and physical plant stimuli utilized by insect herbivores during each of these successive phases (e.g. Kogan, 1977; Rosenthal & Janzen, 1979; Finch, 1980; Miller & Strickler, 1984; Scriber, 1984; Prokopy & Owens, 1983). In most cases, investigators have focused on response of 'normal' or 'representative' individuals of an insect species to one or another sort of plant stimulus. In only a few cases has attention been paid to analysis of intraspecific variation in response pattern (see Papaj & Rausher (1983) for an excellent recent review).

The host range of the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), includes more than 250 species of fruits and vegetables. To locate potential hosts, medfly females are known or believed to respond to the following stimuli: attrac-

tive fruit volatiles (Feron, 1962; Sanders, 1962; Tanaka, 1965); plant color, form, and size (Sanders, 1968b); the form, size, and color of individual fruits, which together elicit attraction after fly arrival on host plants (Feron, 1962; Sanders, 1968b; Nakagawa *et al.*, 1978); contact fruit stimuli (shape, size, color, surface structure, chemical factors) which elicit boring attempts and oviposition (Feron, 1962; Sanders, 1962, 1968a; Tanaka, 1965); and pheromone deposited on the fruit surface after egg-laying which deters repeated oviposition (Prokopy *et al.*, 1978). Except for the last, all of these studies have dealt only with responses of 'normal' or 'representative' individuals.

Here, we compared individual medflies from 3 different populations in propensity to attempt boring into various host fruits.

Materials and methods

The two wild populations of tested flies originated from puparia formed by larvae which infested field-collected fruits of Jerusalem cherry (*Solanum pseudocapsicum*) (ca. 13 mm diam) or loquat (*Eriobotrya japonica*) (ca. 25 mm diam). The infested

Jerusalem cherries were taken at an elevation of ca. 1 500 m from the southeastern slope of Mauna Loa volcano on the island of Hawaii. Jerusalem cherries range in elevation from ca. 1 000–1 700 m on this slope and apparently are the nearly exclusive host of medflies in this isolated habitat. The several-months span in time of fruit ripening of Jerusalem cherries from lower to higher elevations, coupled with the ability of medflies to undergo prolonged quiescence at higher elevations (T.T.Y. Wong, unpubl. data), seemingly has allowed this particular medfly population to become virtually monophagous on this host. Medfly larvae have been detected in only one other host in this habitat: *Myrsine* sp. (fruit = ca. 12 mm diam). Comparatively few have been found in this host (K.Y. Kaneshiro, pers. commun.). The infested loquats were taken at ca. 1 000 m from the Kula area on the western slope of Mt. Haleakala on the island of Maui. This population of medflies had access to a wide range of intermixed or nearby hosts, including citrus (Wong *et al.*, 1983).

The laboratory population of flies tested has been in continuous culture for more than 300 generations at the USDA Fruit Fly Laboratory in Hawaii. Oviposition for the past 100 or more generations has occurred exclusively in holes punctured in 95-cm diameter plastic cylinders.

In each population, both sexes, after eclosion, were maintained together in laboratory cages supplied with food (sucrose and yeast hydrolysate) and water at ca. 20–25 °C and 80–90% RH, and under continuous light. Females were assayed when sexually mature: wild populations when 16–20 days old; the lab population when 9–13 days old. At time of assay initiation, all flies were naive (without previous exposure to any fruit or other oviposition devices).

For assaying, each female was selected at random from a maintenance cage and gently transferred to a test cage devoid of anything except assay fruit. Each was offered (allowed to walk onto) a single uninfested ripe assay fruit and permitted to remain there until it either accepted (attempted boring into) or rejected (left without attempting boring into) the fruit, or until 10 min had elapsed without acceptance or rejection (these data, less than 5% of the total, were excluded from analysis). Each fruit was punctured twice with a needle to facilitate boring attempts. In nearly all cases, acceptance or rejection

occurred within the first 5 min. If a fly attempted boring, it was interrupted immediately and gently removed from the fruit before egg-laying could occur (interval between boring initiation and egg deposition = 20 s or more).

In Exp. 1, each female was offered each of five fruit types: Jerusalem cherry, (Solanaceae) (13 ± 1 mm); grape, *Vitis vinifera*, (Vitaceae) (20 ± 2 mm); loquat (Roseaceae) (25 ± 2 mm); apple, *Malus sylvestris*, (Roseaceae) (60 ± 4 mm); or sweet orange, *Citrus sinensis* (Rutaceae) (75 ± 5 mm). In Exp. 2, each female was offered each of three fruits: mock orange, *Murraya paniculata*, (Rutaceae) (10 ± 1 mm); kumquat, *Fortunella japonica*, (Rutaceae) (20 ± 2 mm); or grapefruit, *Citrus paradisi*, (Rutaceae) (115 ± 10 mm). For each female, we waited 3 min between departure or removal from one fruit until offering the next.

To minimize experimental error, we (a) assayed successively no more than 5 (Exp. 1) or 6 (Exp. 2) individuals from one population before assaying 5–6 individuals from a different population, (b) ensured that for each population, each fruit type was represented an equal number of times in the 1st, 2nd, etc. positions of the assay sequence, and (c) offered the same fruit specimen an equal number of times (usually no more than three) to flies of each population. Use of these procedures resulted in comparatively little intra-population variation in response pattern from one group of 5 (Exp. 1) or 6 (Exp. 2) flies to the next (Table 1).

Results

The results (Table 1) reveal several differences among the three populations in host acceptance pattern. In Exp. 1, flies originating as larvae from Jerusalem cherry (Jerusalem cherry flies) had a significantly greater propensity to accept Jerusalem cherry and grape than loquat, apple, or sweet orange. Flies originating as larvae from loquat (loquat flies) exhibited a host acceptance pattern similar to Jerusalem cherry flies. Lab flies, however, accepted all five hosts about equally. These results led us to conduct the 2nd experiment, in which we offered three rutaceous fruit types of highly divergent size. Here (Exp. 2), Jerusalem cherry flies accepted mock orange and kumquat equally, and each of these significantly more often than grape-

Table 1. Acceptance of various fruit types by *C. capitata* females of different populations.

Exp.	Population	No. assayed	Females accepting fruit (%) ¹				
			Jerusalem cherry (13 mm) ²	Grape (20 mm)	Loquat (25 mm)	Apple (60 mm)	Sweet Orange (75 mm)
1	Jerusalem cherry	70	76 ± 6a	71 ± 7a	53 ± 8b	43 ± 5b	39 ± 8b
	Loquat	70	68 ± 6ab	73 ± 5a	56 ± 8b	61 ± 7ab	54 ± 7b
	Laboratory	70	86 ± 5a	93 ± 3a	94 ± 2a	94 ± 3a	86 ± 5a
2			Mock Orange (10 mm)	Kumquat (20 mm)	Grapefruit (115 mm)		
	Jerusalem cherry	42	79 ± 6a	79 ± 6a	36 ± 9b		
	Loquat	42	50 ± 11b	79 ± 4a	24 ± 3c		
	Laboratory	42	62 ± 5b	93 ± 5a	79 ± 7ab		

¹ Data are given as mean % acceptance ± standard error. For each treatment, these values were determined through separation of flies of each population into 14 groups of 5 each (Exp. 1) or 7 groups of 6 each (Exp. 2) (see Methods section for further explanation). Values in each line followed by the same letter are not significantly different (G-test at the 0.05 level).

² Mean diameter of assayed fruit.

fruit, whereas loquat flies accepted kumquat significantly more often than either mock orange or grapefruit. Lab flies accepted kumquat significantly more often than mock orange, but neither of these significantly more often than grapefruit.

Discussion

The pattern in which hosts were accepted or rejected by flies of each medfly population assayed here suggests that fruit size had a strong influence on acceptance pattern, while fruit taxonomic status had little effect. To illustrate, grape and kumquat fruits (similar size but different families) were about equally acceptable to wild flies, whereas kumquat and grapefruit (same family but different size) were unequally acceptable. In addition, Jerusalem cherry flies (originating from 13 mm fruit) had a much greater tendency to accept Jerusalem cherry and other fruits slightly larger (grape, 20 mm; kumquat, 20 mm) or slightly smaller (mock orange, 10 mm) than to accept fruits substantially larger (loquat, 25 mm; apple, 60 mm; sweet orange, 75 mm; grapefruit, 115 mm). Loquat flies (originating from 25 mm fruit) accepted Jerusalem cherry, grape, and kumquat about equally and more often than any of the four larger fruits. They were, however, less prone than Jerusalem cherry flies to accept the

smallest fruit, mock orange. In contrast, the lab flies, whose progenitors had oviposited in 95 mm plastic cylinders for at least 100 successive generations, had about an equally high propensity to accept all fruit types tested except the smallest, mock orange. Previously, Sanders (1968a) found that medflies of a population cultured artificially (for an unknown number of generations using containers of unknown size to collect eggs) attempted boring more often into 20–60 mm artificial fruit models than into 10 or 80 mm ones. Studies on other tephritids, such as *Rhagoletis cerasi* L., *R. pomonella* (Walsh), *R. mendax* Curran, *R. zephyria* Snow, and *R. cornivora* Bush, likewise revealed the existence of a particular range of fruit sizes, varying according to fly species, which elicited the greatest acceptance (Prokopy & Boller, 1971; Prokopy & Bush, 1973).

Whether the detected variation in host acceptance pattern among the three medfly populations assayed here was largely or totally due to genetic differences between the populations is uncertain. However, the fact that all flies were naive (no previous exposure to fruit) when assays were initiated rules out adult conditioning (Prokopy *et al.*, 1982a) as a contributing element. Also, the fact that Jerusalem cherry flies accepted grape and kumquat equally as well as they accepted Jerusalem cherry (each fruit is a member of a different family), and that loquat flies accepted Jerusalem cherry, grape,

and kumquat to a greater degree than loquat, suggests that larval conditioning had little or no effect.

It seems probable, therefore, that genetic differences in host fruit acceptance propensity do exist between the essentially monophagous Jerusalem cherry population, the polyphagous loquat population, and the lab cultured population which partially or fully account for the results obtained. Attempts are now underway to firmly establish whether this indeed is the case. In a recent study, genetic differences between populations of *R. pomonella* flies were believed to account for some, if not most, of the observed inter-population variation in host acceptance pattern found in that species (Prokopy *et al.*, 1982b). Perhaps for several phases of the host finding process in medflies and other tephritids, there exists greater variation in inter-population response patterns than is presently realized.

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Zusammenfassung

Unterschiede in der Art der Wirtsannahme zwischen Populationen von Ceratitis capitata-Imagines

Bei zwei Wildherkünften und einem Laboratoriumsstamm von *Ceratitidis capitata* wurden Weibchen auf ihre Neigung zur Probebohrung in Früchte vor der Eiablage untersucht; dabei ergaben sich gesicherte Unterschiede zwischen den Populationen. Die Resultate deuten drauf hin, (a) dass die Fruchtgrösse einen grossen, und die taxonomische Stellung der Früchte einen kleinen Einfluss auf das Annahmemuster der Populationen ausübt, und (b) dass mindestens ein Teil der Unterschiede zwischen den Populationen genetisch bedingt ist.

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